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Evolution of reproductive phenology in annual social insects competing for floral resources

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ABSTRACT

Question: How does reproductive timing in annual social insects evolve under intraspecific exploitation competition and in response to a changing environment? The latter includes shifts in resource abundance, mortality, season length, and resource peak timing, factors often associated with climate change.

Background: Climate and land use are changing. Evolutionary ecology must learn to predict how organisms are affected by, and might adapt to, such changes. Classic theory predicts how the timing of reproduction in organisms with an annual life-cycle (including many plants and social insects) optimally balances their phases of growth and reproduction with seasonal resource distributions. But theory has yet to take into account interactions within or between species.

Method: We use invasion analysis to calculate the evolutionarily stable reproduction time by extending a classic model of annual social insects (such as bumblebees) to include competition for seasonally variable resources. There are two types of (colony) production: vegetative (workers) and reproductive (queens). The initial worker density in the landscape depends on the density of the surviving queens from the previous year. Reproduction time is approximated as a sudden (bang-bang) switch from vegetative to reproductive production during the season. We compare the evolutionarily stable strategy (ESS) with the classical optimization result without competition. We also compare it with the strategy that maximizes population size under resource competition.

Results and conclusions: Under resource competition, the ESS reproduction time occurs earlier than the optimum predicted by classic theory. But the ESS is later than the strategy that maximizes population size. Thus phenological adaptation to environmental change is likely to reduce population sizes. Both the ESS and the optimal reproductive time change more slowly than do shifts in seasonal resource peaks. Hence a growing asynchrony between peak flowering times and the timing of bumblebee reproduction – often interpreted as a phenological mismatch – may actually be an adaptive response of pollinators in this system.

Keywords: adaptive dynamics, annual social insect, bumblebee, climate change, phenological mismatch, reproductive phenology, resource competition.

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INTRODUCTION

The life-cycle of an annual organism can be viewed as a solution to the problem of maximizing fitness by a suitable timing of growth and reproduction. The optimal timing of these phases (the optimal phenology) depends on seasonal variations of abiotic factors, such as temperature, snow melt dates, and water availability, and biotic interactions, such as competition, pollination, and predation. A species' phenology may thus be affected by environmental change, including changes in climate and land use. Climate-driven changes in species' phenology is a global and well-documented phenomenon (Parmesan and Yohe, 2003; Menzel *et al.*, 2006), but relatively little is known about the fitness consequences of these changes (e.g. Ramula *et al.*, 2015), and we are thus ill-prepared to predict which phenological strategies will be successful in future environments. Changes in land use may also have large effects on the fitness and phenology of an annual organism. Therefore, it is essential to consider the link between phenology, environmental variation, and life-history optimization (see, for example, Forrest and Miller-Rushing, 2010).

Classic theory on the optimal energy allocation for annual organisms, including annual plants (Cohen, 1971) and annual social bees (Macevicz and Oster, 1976), predicts that reproductive output is maximized by first using the available resources for growth, and then switching to reproductive growth, a so-called 'bang-bang' strategy. This theory can be used to calculate how the optimal switching time depends on the seasonal distribution of resources (Macevicz and Oster, 1976; Johansson *et al.*, 2013). For example, Macevicz and Oster (1976) showed that optimal switching time from worker to queen production was delayed by increased productivity or by a later resource peak. Theoretical work has also demonstrated that factors such as internal growth constraints and stochastic fluctuations may complicate the picture by selecting for simultaneous investment into growth and reproduction (King and Roughgarden, 1982; Mitesser *et al.*, 2007; Poitrineau *et al.*, 2009) as opposed to a bang-bang strategy. Internal growth constraints may further influence how changes in the seasonal environment affect colony growth in annual social insects (Hovestadt *et al.*, 2019) and optimal phenological shifts in annual plants (Lindh *et al.*, 2016).

Available theory mainly considers optimal reproductive allocation in a single organism. It does not take into account that growth factors – in particular resource availability – might be affected by intra-specific competition. For example, even if day lengths and light intensity increase as spring progresses, light levels received by a specific plant on the ground may decrease as competing plants leaf out. It follows that the strength of competition is expected to vary over the season, depending on the population sizes of the competitors and their phenological strategies. Therefore, phenological adaptation not only depends on how organisms are affected by resource seasonality, which is the starting point for classic optimization theory, but also on how the organisms in turn dynamically influence the resource availability. A situation where the environment is dictated by the strategies used by the players can typically not be treated as an optimization problem, but rather needs to be analysed as an evolutionary game (Metz *et al.*, 2008).

An annual social insect such as the bumblebee has several characteristics that can motivate a game-theoretical approach to study its phenology: (1) they depend strongly on seasonally variable resources, specifically pollen and nectar from various plant species with differing flowering times; (2) they have an annual life-cycle for which much optimization theory already exists and provides a solid ground for further theoretical development; and (3) they can consume a very large proportion of the daily produced floral resources available to them (Heinrich, 1976), indicating that exploitation competition may strongly influence resource availability at any point in time. The only model considering population and colony dynamics with competition for resources in a foraging landscape is *Bumble*-BEEHAVE, an agent-based model by Becher *et al.* (2018). However, evolution has yet to be considered in agent-based bumblebee population models with resource competition, thus hindering long-term predictions.

How bumblebees are affected by resource variation is important in the context of global pollinator decline (Potts *et al.*, 2010) due to, for example, landscape fragmentation, agrochemicals and pathogens (Williams and Osborne, 2009), and changes in the seasonal availability of flower resources (e.g. Fitzpatrick *et al.*, 2007; Burkle *et al.*, 2013). It is, however, hard to predict how bumblebee populations respond to changed resource availability, as it may depend on which part of their annual cycle is affected as well as on competition. Variation in food availability late in the season is known to have a strong effect on the reproductive output (Rundlöf *et al.*, 2014). In agricultural landscapes, there are usually strong resource peaks early in the season during the bloom of, for example, oilseed rape or apple. Such early resource peaks may increase the growth of a colony, but not necessarily its reproductive output in terms of queens and males (Westphal *et al.*, 2009). An early mass-flowering crop allows many colonies to establish in an area, but a lack of resources later in the season in combination with strong competition among the colonies may hamper their reproductive success (Galpern *et al.*, 2017). Furthermore, resource competition between the domesticated honey bee and bumblebees has been highlighted as a likely cause of the decline of bumblebees (Goulson, 2003; Goulson and Sparrow, 2009; Herbertsson *et al.*, 2016), which further underscores that bumblebee populations are affected by resource competition in general.

The purpose of this paper is to clarify the evolutionary impact of exploitation competition on reproductive phenology under various scenarios of environmental change. To this end we devise an eco-evolutionary model inspired by bumblebees which extends previous models by accounting for competition for seasonal resources among growing colonies, as well as between-year population dynamics. We focus on the switching time from worker to queen production (i.e. the reproduction time), assuming that floral resources are the limiting factor, and ignoring constraints posed by the egg-laying rate of the queen (cf. Beekman *et al.*, 1998). Four environmental factors related to climate change and land-use change in temperate regions are considered: resource abundance, mortality rate, season length, and the timing of seasonal peaks. We will in particular study the evolutionarily stable strategy (ESS) in these different scenarios, to obtain an evolutionary understanding of which phenological strategies might be favoured in the future. We will also compare the ESS to the reproduction time maximizing population size (Pop Max), and the optimal reproduction time if competition is ignored (*sensu* Macevicz and Oster, 1976). These comparisons will provide predictions of how bumblebee populations may respond to climate and land-use changes in the short term, depending on which phenological strategy they currently employ, or in the longer term, via changes in the phenological strategy due to local adaptation or invasions of pre-adapted species from other geographic regions.

METHODS

We extend an earlier optimization model of an annual social insect (Macevicz and Oster, 1976; Oster, 1976) by introducing resource competition and ecological feedback. We focus on the switch from worker to queen production, which we define as the reproduction time and assume is immediate (bang-bang). Resource competition is based on the daily competition for resources (nectar and pollen), which we assume are reset every morning to a level that can vary across the season. We consider a whole population of growing colonies that compete for the same resources and the growth of that population from one season to the next. The ecological equilibrium established over many seasons serves as the basis for an invasion analysis which evaluates the fate of invading mutants and calculates the ESS switching time.

Daily floral resource competition

We assume that a number of workers W in a given area compete for a common floral resource of pollen and nectar R. We let $\mathrm{d}R(\tau)/\mathrm{d}\tau = -aR(\tau)W$ describe the daily resource depletion, where τ is the time of the day in units of days, a is the feeding rate per worker per day, and $R(0)$ is the abundance of resources at the beginning of the day. The solution to the differential equation is $R(\tau) = R(0)\exp(-aW\tau)$, and the total resource intake per day is $R(0) - R(1) = R(0)(1 - \exp(-aW))$. We can now define the resource intake per worker per day $F(t) = r(t)f(W(t)) = R(0)(1 - \exp(-aW(t)))/W(t)$, where t is the time in the season, $f(W(t)) = (1 - \exp(-aW(t)))/W(t)$ is the realized feeding rate (per day), taking density dependence into account, and $r(t) = R(0)$ is the amount of resources available at the beginning of the day. We assume that the flowers refill the nectar during night-time (Heinrich, 1976) and, consequently, $R(0)$ does not depend on the consumption the previous day. To start with, we assume that the maximum resource abundance $R(0)$ is constant over the season, and later we let it vary over the season and set $R(0) = r(t)$.

Seasonal colony dynamics

Following Macevicz and Oster (1976), we let the number of new queens define the reproductive output of the colony and ignore males, which tend to be produced continuously (Duchateau and Velthuis, 1988). There are thus only workers and queens in our model and the colony switch from worker to queen production occurs at time t_S. This switching time is assumed to be a heritable evolving trait, and is referred to as the reproduction time. The shape of the control function $u(t)$, where $u(t) \in [0, 1]$, can in principle also evolve (cf. Poitrineau *et al.*, 2009), but here we assume that $u(t) = 1$ when $0 \le t < t_S$ and $u(t) = 0$ when $t_S \le t < T$. We assume that this bang-bang strategy is evolutionarily stable. The start and end times of the colony are fixed to 0 and T, respectively, such that the season length is T (Fig. 1). The colony dynamics is described by two coupled ordinary differential equations:

$$\begin{aligned} \frac{\mathrm{d}W(t)}{\mathrm{d}t} &= W(t)F(t)u(t) - m(t)W(t) \\ \frac{\mathrm{d}Q(t)}{\mathrm{d}t} &= W(t)F(t)(1 - u(t)) - m(t)Q(t). \end{aligned} \tag{1}$$

Here, $W_0 > 0$ is the initial number of workers and $Q_0 = 0$ is the initial number of queens. We assume that the resources are measured in such units that $F(t)$, the resource intake per worker per day, directly translates to new workers or queens. In other words, we interpret $F(t)$ as fecundity. The mortality m can vary seasonally due to, for example, pesticide

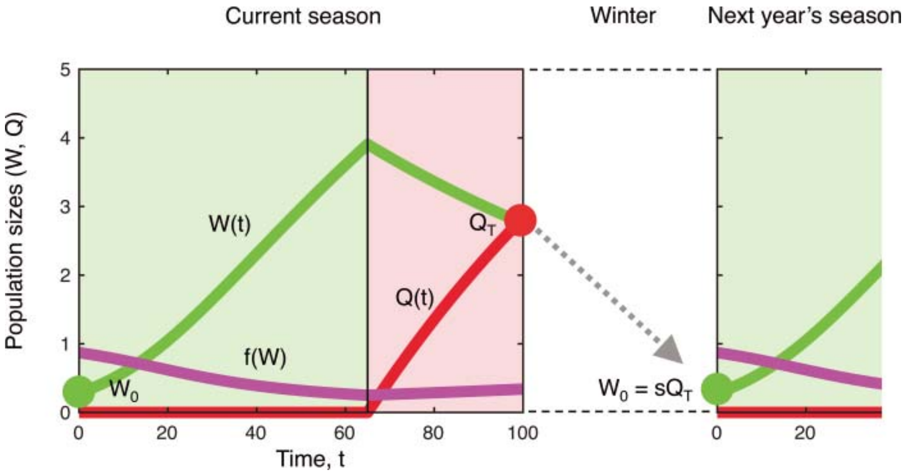

Fig. 1. Initially at time $t = 0$, the worker population $W(t)$ is W_0. From time $t = 0$ to time $t = t_S$, all the collected resources are devoted to worker production. As a result, the worker population size (green line) at first grows almost exponentially, but as competition for the floral resources increases, the growth rate decreases. The available resources $f(W)$ are inversely related to the number of workers (magenta line). At time $t = t_S$, the colony switches to queen production, resulting in an increasing queen population size (red line) for the remaining season. Since the worker population is decreasing due to background mortality, the queen production rate also decreases towards the end of the season. The ecological equilibrium is defined by $W_0 = sQ_T$, and this population size is a convergent fix point found by an iterative process illustrated by the arrow.

treatments or variable predation pressures. Note that $W(t)$ and $Q(t)$ in our model describe the population sizes in a given area in the landscape, and not the population size of a single colony as in the colony model of Macevicz and Oster.

Ecological equilibrium

By the end of the season, the fertilized queens $Q_T = Q(T)$ enter diapause, and the surviving queens next season is sQ_T, where s is the probability to survive the winter. We find the ecological equilibrium population density by iterating until the initial worker population W_0 converges to the fixpoint W_0^*, where $W_0 = sQ_T$. We let $W^*(t)$ and $Q^*(t)$ denote the seasonal density of workers and queens at that equilibrium. This constitutes the equilibrium competitive environment where mutant strategies are evaluated. We define the Pop Max strategy as the reproductive timing t_S that maximizes W_0^*.

Evolutionary dynamics and invasion fitness

According to the framework of adaptive dynamics, we assume that the evolutionary dynamics is described by the competition of residents and mutants (Geritz *et al.*, 1998). Only the common residents, with switching time t_S, influence the environment, whereas the rare mutants, with switching time t'_S, are growing in the equilibrium environment set by the residents $F^*(t) = r(t)(1 - \exp(-aW^*(t)))/W^*(t)$. The colony dynamics of the mutant is described by two coupled ordinary differential equations which depend on the resident equilibrium population $W^*(t)$:

$$\begin{aligned} \frac{\mathrm{d}W'(t)}{\mathrm{d}t} &= W'(t)F^*(t)u'(t) - m(t)W'(t) \\ \frac{\mathrm{d}Q'(t)}{\mathrm{d}t} &= W'(t)F^*(t)(1 - u'(t)) - m(t)Q'(t). \end{aligned} \tag{2}$$

At the start of the season, the mutant population size is set to 1 and the invasion fitness is therefore $w(t'_S, t_S) = sQ'_T$, which is equivalent to the mutant per capita growth rate per year when the resident is at equilibrium (Geritz *et al.*, 1998). If the invasion fitness is above 1, the mutant will invade, otherwise the mutant will go extinct. We will primarily seek the strategy that cannot be beaten by any other strategy, the evolutionarily stable strategy (ESS).

Parameters

The following parameter values were chosen to characterize a general bumblebee colony. We choose a season length of $T = 100$ days representing the summer months of June, July, and August in Scania, in southern Sweden. We estimate that 10% ($s = 0.1$) of the queens survive to the next season, i.e. successfully mate, hibernate, and build a new nest. With a resource abundance of $r = 0.1$ per day, an average worker collects at a maximum resources for a new bumblebee in about 10 days. With a mortality of $m = 0.01$ per day, an average bumblebee survives about 100 days. Flower resource abundance can be measured in units such that $a = 1$.

Analysis overview

In the following analysis we will: (1) characterize the ESS timing of reproduction and compare it with the Pop Max (the population maximum) and the M&O optimum (Macevicz and Oster, 1976); (2) elucidate the importance of resource and mortality variation; (3) study the evolutionary responses to increasing season length on a calendar scale; and (4) analyse the effects of resource and mortality peak timing.

RESULTS

The ESS, Pop Max, and M&O solutions

Figure 2 illustrates the mechanisms of frequency- and density-dependent selection in our model. In each panel, a single resident strategy is tried against a suite of potential invading mutants. The invading mutant populations are all rescaled such that the size of the queen population at the end of the season can be used as a fitness proxy, comparing mutants with each other and with the resident.

Figure 2a shows the case of a relatively early switching resident type. An early switching results in a modest worker population at the end of the season and relatively little competition for resources (magenta line). An even earlier switching mutant will pay the price of a smaller worker population and not be able to fully exploit the available resources. It will have a smaller queen population than the resident strategy at the end of the season, i.e. a lower fitness. A later switching mutant, however, will be able to grow a substantially larger

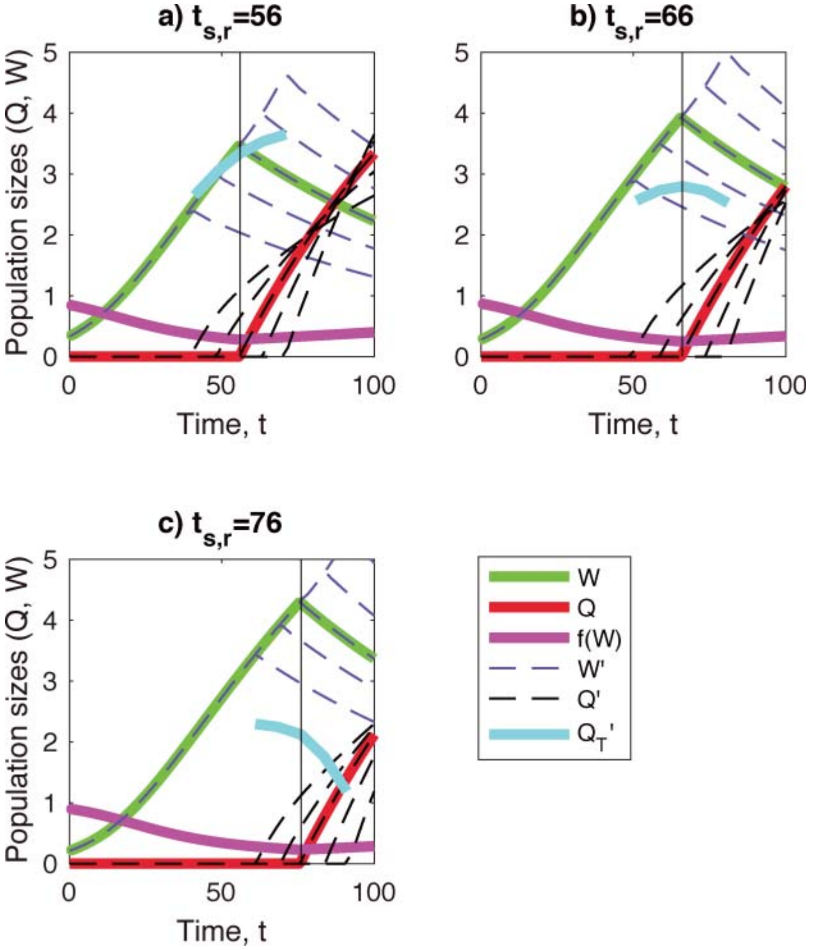

Fig. 2. Mutants (thin lines) trying to invade residents (thick lines). In (b) the resident is at the ESS, but not in (a) and (c). The resident worker population W (green line) is consuming the available resources, which are constant in this figure. We define the available resource per capita, i.e. the environment set by the resident, by $f(W)$ (magenta line). The resident queen population size Q (red line) by the end of the season is the reproductive output Q_T. The mutant worker population W_m (black dashed lines) and the mutant queen population Q_m (blue dashed lines) are growing in the resident environment. The mutant queen population size by the end of the season Q'_T is used to define the mutant invasion fitness $w(t'_S, t_S) = sQ'_T$. The invasion fitness is described by the cyan line, which is mapping the switching time t_S to the mutant queen production Q'_T by the end of the season ($T = 100$).

worker population and use that to raise even more queens than the resident. There is thus selection for later switching times (cyan line).

In Fig. 2c we see a different situation. The resident population switches to reproduction very late in the season, when it has built a large worker population (green line). This creates strong competition for resources (magenta line), but also leaves very little time for queen production. A mutant switching earlier will have a smaller worker population, but will have more time to produce queens and in the end will be favoured by selection (cyan line).

Figure 2b, finally, shows the ESS situation. No mutants can invade. In Appendix A (evolutionary-ecology.com/data/3199Appendix.pdf) we show that the ESS switching time can be found by solving

$$\int_{t_s}^{T} F^*(t)dt = 1. \tag{3}$$

for t_S. At ESS, the population switches to queen production when a new worker on average will produce only one new queen during the rest of the season (cf. Poitrineau *et al.*, 2009).

One noticeable feature of Fig. 2 is that the resident population, measured either as the number of workers at $t = 0$ or the number of queens at $t = T$, declines monotonically when shifting from an early switching resident (Fig. 2a) to later switching times (Fig. 2b,c). The ESS strategy (Fig. 2b) does not maximize population size. The explanation lies in how frequency dependence works in this model. If a single colony delays reproduction, it will produce more workers, which will further deplete resources during the rest of the season. The cost of this increased competition is paid by all colonies, whereas the delaying colony single-handedly reaps the benefit of a larger worker population. This 'tragedy of the commons' mechanism intuitively explains why the ESS is always later than the Pop Max strategy, maximizing population size (shown in Appendix A). The switching strategy that maximizes total population size can always be exploited by a single mutant colony with a later switching time.

Another comparison can be made with the optimal strategy in a model without resource competition (M&O). If resources are not depleted by a growing worker population, it will pay off to wait even longer before switching to reproduction. The equation for the ESS above still holds, but the resource availability $F(t)$ is not affected by the resident population, and will therefore be larger, which means that t_S^* will be later. This intuitively explains why the M&O solution is always later than the ESS in our model. The ESS is in this way always positioned between the early Pop Max strategy and the late M&O strategy.

Dependence of the ESS on resource abundance and mortality

The evolutionary response of the reproduction time to changes in resource abundance and mortality very much depends on resource competition and frequency-dependent selection. We here assume that the resource abundance and the mortality rate are constant throughout the season. Large environmental variation influencing the whole season represents, for example, global warming or changes in pesticide use.

Increasing the resource abundance uniformly over the season will advance the ESS and Pop Max strategies and delay the M&O strategy (Fig. 3a). It can be shown that as the resource abundance tends to infinity, the ESS converges to an intermediate strategy whereas the Pop Max strategy tends to the start of the season and the M&O strategy converges to the end of the season (Appendix B). Increasing the resource abundance causes an increasing equilibrium population size (shown as increasingly lighter shading in Fig. 3a), but competition also implies lower available resources for the remaining season. This explains why the ESS and Pop Max strategies are to reproduce earlier as the resources are increasing whereas in the absence of competition a higher resource always gives a delayed reproduction time (M&O model, Appendix A). Since the ESS tends to an intermediate solution between the M&O strategy and the Pop Max strategy, it is the strategy least sensitive to resource abundance change (Fig. 3a).

Similar to these results, Lindh *et al.* (2016) showed that increased productivity may select for an advanced flowering time in annual plants when plant growth is constrained, for example due to self-shading. Here we assume that the floral resources for the bumblebee colony are reduced by competition, particularly late in the season, which gives a similar growth constraint for the individual colony as in Lindh *et al.* (2016) and explains the similar outcomes.

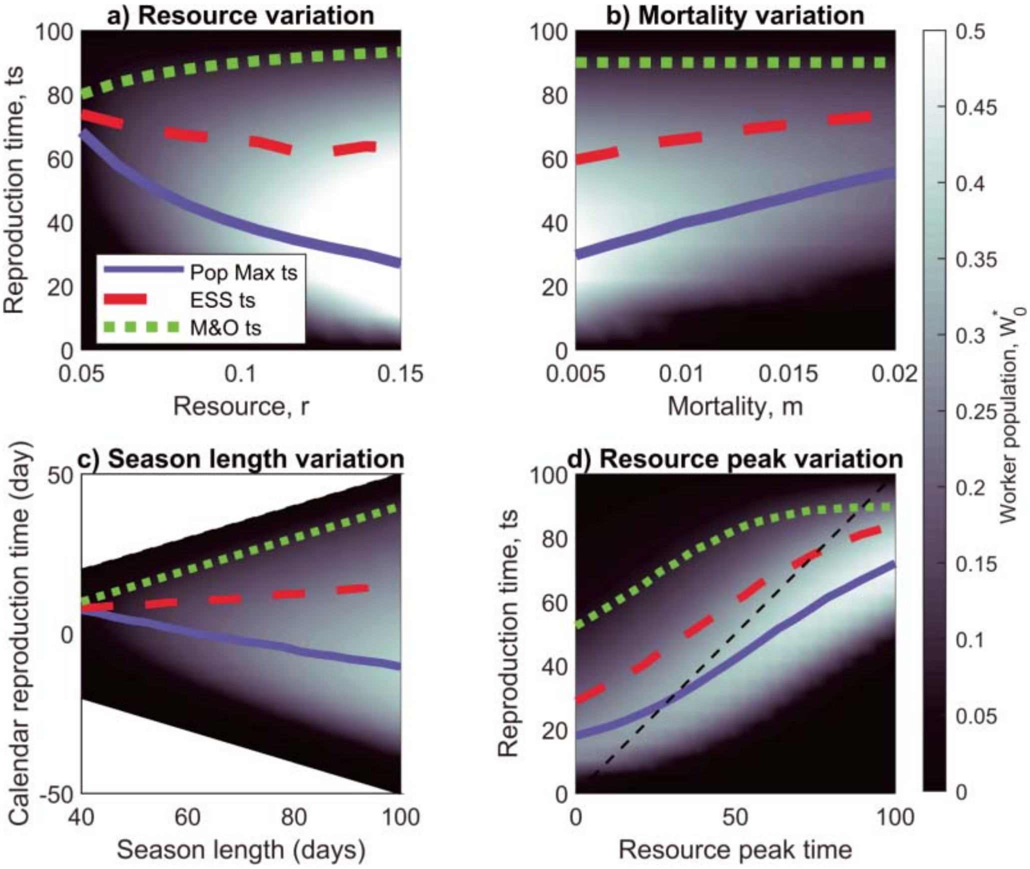

Fig. 3. Effects of environmental variation on the reproduction time and reproductive output. (a) The trend of the ESS (dashed red line), and that of the Pop Max strategy (solid blue line), with resource competition, are going in the opposite direction to the M&O optimum without resource competition (green dotted line). The ESS lies between the M&O optimum and the Pop Max strategy, and is converging to an intermediate time. (b) Under increasing mortality, both the ESS and Pop Max converge towards the M&O optimum. (c) Season length influences the reproduction time differently depending on resource competition and the model. The ESS and the M&O optimum both have a delayed reproduction time, which is the opposite to the Pop Max strategy. (d) A later resource peak time delays the ESS, the Pop Max strategy, and the M&O optimum. All strategies are positively correlated with the resource peak time. The highest population is found at a late resource peak time. Note that for the M&O optimum (green dotted line), the population is independent of the resource peak time (Appendix A). The initial worker population at equilibrium W_0* is shown in the background. Default values: $m = 0.01$ and $r = 0.1$.

The response of the ESS and the Pop Max strategy to an increasing mortality is basically the opposite to an increasing resource abundance *r*, and consequently both are delayed (Fig. 3b). We also find that the population collapses ($W_0^* = 0$) at low resource abundance and high mortality.

Dependence of the ESS on season length

The effect of longer growth seasons on bumblebee timing and populations is largely unknown, but it is reasonable to assume that the beginning of the colony is advanced, and that the end of the colony is delayed. As a first approximation, we assume here that the resource level is fixed throughout the season, i.e. $r(t)$ is constant. Note that a longer season implies a larger total amount of available resources, integrated across the season. We assume a season of length T on a calendar timeline that is symmetric around $t = 0$ starting at time $-T/2$ and ending at time $T/2$.

Our analysis shows that on a calendar timescale, both the ESS and the M&O optimum are delayed by an increasing season length (Fig. 3c). For the M&O model, the time between the reproduction time t_S and the end of the season is constant (Appendix A). The ESS shows a weaker response, however, because of increased late-season competition. Specifically, as the total amount of resource increases (the larger integral of the constant resource), the abundance of workers also increases, implying heavier resource depletion towards the end of the season.

In contrast to the ESS and M&O optimum, the Pop Max strategy is advanced by an increased season length (Fig. 3c). In other words, a population which switches early to reproduction will achieve a high population size by avoiding depletion of late-season resources and spending a long time producing queens.

Dependence of the ESS on the timing of a seasonal resource or mortality peak

Populations of many bumblebee species are tending to decrease in modern agricultural landscapes (Fitzpatrick *et al.*, 2007; Bommarco *et al.*, 2012) despite the widespread availability of flowering crops such as oilseed rape (Westphal *et al.*, 2009; Holzschuh *et al.*, 2016). In natural meadows and traditional farming landscapes, the flowering resources are more evenly spread out over the season, compared with flower resources in modern agricultural landscapes. This suggests that not only the abundance of the resource matters for bumblebee population densities, but also the timing of the resource (Schellhorn *et al.*, 2015).

We describe the resource abundance peak by a Gaussian function (with a variance of 1000 and a standard deviation of $\sqrt{1000} \approx 32$) scaled such that the integral of $r(t)$ in the interval $t \in [0, T]$ is constant. The resulting optimal strategies are shown in Fig. 3d. As expected, there is a strong correlation between the resource peak time and the optimal reproduction time. All analysed strategies (Pop Max, ESS, and M&O) are delayed as a response to a delayed resource peak.

By viewing the dashed diagonal black line in Fig. 3d we see that both the ESS and Pop Max strategy reproduction time is later than the resource peak if the resource peak is early, and vice versa if the resource peak is late. This lag in response can be explained by constraints posed by the season. The reproduction time can neither be too early, as this would imply little time for worker population growth, nor too late, as this would imply too little time to produce queens. A resource abundance Gaussian with a lower variance will follow the dashed diagonal line more closely, and will therefore reduce the lag in response.

The M&O model without mortality predicts that the reproductive output at the optimal strategy is independent of the resource distribution (Appendix A). In contrast, under competition, the equilibrium population size is largest for late resource peaks (Fig. 3d). The reason for this is that a late resource peak is more useful for the colonies than an early resource peak, since a colony worker population is always larger by the end of the season, compared with the initial population (Fig. 2).

It can also be noted that for populations at the ESS, the short-term effects of a small delay (advance) in the resource peak will be an increase (decrease) of the population size, assuming that the reproduction time remains unchanged. Long-term effects of resource peak variations will, however, be more moderate, assuming that the reproduction time follows the ESS curve (red dashed line).

In Appendix C, we show that the reproduction time is almost independent of a Gaussian mortality peak, but populations are clearly lower for a late mortality peak. This is in line with the earlier observation that a late resource peak is more useful for the colonies than an early resource peak.

DISCUSSION

Although data relating to phenological responses to climate change is abundant, the long-term consequences of these changes are difficult to predict. Evolutionary and ecological theory can, however, yield insights into how species are expected to adapt their phenology and respond demographically under different scenarios of environmental change. In this vein, we here extended a classic optimal control model of an annual social insect by Macevicz and Oster from 1976 (M&O) to include within-season competition for floral resources and between-year population dynamics. Our analysis shows that the ESS timing of reproduction generally occurs earlier than the optimal M&O reproduction time (Appendix A), implying that resource competition and density dependence select for an earlier timing of reproduction.

One interpretation of the assumptions in the M&O model, as well as ours, is that egg-laying rates increase with the amount of resource intake to the colony (eq. 2). Beekman *et al.* (1998) analysed an alternative model assuming fixed egg-laying rates, in line with evidence from experimental studies (e.g. Duchateau and Velthuis, 1988), and concluded that this leads to an earlier timing of reproduction compared with the predictions of Macevicz and Oster. Hence this result by Beekman *et al.* (1998) also has some empirical support from experimental studies showing that the onset of reproduction occurs relatively early in the bumblebee colony cycle (Müller *et al.*, 1992). The fact that colony sizes and thus egg production show large variation across species of bumblebees (Cueva del Castillo *et al.*, 2015) indicates that egg-laying rate is not a limiting factor for colony growth in general. Our analysis thus suggests that competition for resources may provide an alternative explanation for why reproduction occurs relatively early in the colony cycle.

Below, we will discuss our model predictions regarding adaptive responses to changing climates and outline how our model can be used to predict and understand short- and long-term population trends in this context.

Effects of competition on adaptive responses to climate change

Competition for resources has a clear impact on how reproduction time is expected to adapt in several of the generic scenarios of climate change we consider in this study. Specifically, the ESS reproduction time (with resource competition) and the M&O optimum (without competition) respond in distinctly different ways to changes in resource abundance (delayed vs. advanced), mortality (advanced vs. unaffected), and increased season length (slightly vs. markedly delayed). In all these cases, the differing outcomes can be understood by considering the effects of environmental changes on late-season resource levels via changes in population densities and competitive pressure.

Increased resources and longer seasons increase late-season competition, which explains why the ESS responds in the opposite direction or at a slower rate than the M&O optimum under these two types of changes. The delayed ESS under increased mortality, finally, occurs because of reduced late-season competition. Thus, our model predicts that natural selection will favour earlier reproduction times when resource abundance increases, and later reproduction times when background mortality increases, for example by pesticide use (Bryden *et al.*, 2013).

In the scenario with a shifting resource peak, the ESS reproductive time and M&O optimum responded in the same direction and roughly similar rate (Fig. 3d), indicating that the effect of competition does not interact with the effect of a shifting resource peak. It should be noted, however, that the ESS reproductive time and M&O optimum do not change in parallel with the resource peak but at a slower rate (Fig. 3d) depending on the constraint posed by the start and end of the season. This finding also implies that reproductive timing in annual social insects may not follow the heuristic 1 : 1 rule (Visser and Both, 2005), which posits that consumers should change their phenology at the same rate as their resource to avoid mismatch. Rather, our analysis indicates an ‘adaptive phenological mismatch’ (Visser *et al.*, 2012) between the reproductive timing and the seasonal resource peak. Such an adaptive mismatch has to our knowledge not been previously considered in the context of pollinators and flowering plants (Hegland *et al.*, 2009).

Pyke *et al.* (2011) analysed how plant phenology and bumblebee phenology were affected by an altitudinal gradient. They found, in line with their expectations, that flowering and bee emergence occurred at a later time at higher elevations, but that workers showed a stronger response than the males. The authors suggested that the weaker response of the males was due to interrupted sampling at the end of the season, but if the males indeed show a weaker response it is interesting to compare their finding with our study. Assuming that the emergence of males accurately reflects a switch to reproduction, and the season length becomes shorter at higher elevations, these observations agree with our finding that the ESS reproduction time is only slightly affected by a shorter season compared with worker emergence, which in our model occurs at the start of the season (Fig. 3c). In contrast to the finding by Pyke *et al.* (2011) that males occur later in the season at higher altitudes, the ESS reproduction time is weakly advanced by a shorter season in our model. On the other hand, our model also predicts that a later flowering peak selects for a delayed ESS reproduction time. Therefore, if the shorter season length is accompanied by a later flowering peak, our results could potentially be reconciled with the observed weak delay of male emergence, and it is interesting to note that Pyke *et al.* indeed observed a later flowering peak at higher elevations.

Demographic effects of adaptation to changing climates

We find that the ESS reproduction time is always later than the Pop Max strategy (Fig. 2 and Appendix A). Evolution is in other words not maximizing population size. Because the ESS and Pop Max reproduction times are different, our model predicts that short-term and long-term demographic responses to changed climate variables may proceed in different directions.

We do not expect any significant evolution to occur under climate change on the short-term perspective. In Fig. 3, such short-term effects correspond to variations in the environmental factor (i.e. a horizontal variation in Fig. 3). On the long-term perspective, we can expect species to adapt to the changing climate, i.e. follow the ESS curve. By comparing the ESS and the Pop Max we can predict how changes in the climate will influence the population size, shown in the background of the figures. For example, a population at the ESS will benefit temporarily from a delayed resource peak, which can be seen by moving horizontally to the right in Fig. 3d, starting somewhere at the ESS curve. In contrast, long-term population sizes are less influenced by changes in resource peak time, as can be seen by following the ESS curve in Fig. 3d.

Apart from climate change, these contrasting short- and long-term responses to shifting resource peaks are also interesting to consider in relation to changing seasonal distributions of floral resources due to modern agriculture. Previous rural landscapes had a more even distribution of floral resources and for example red clover production was an important resource for pollinators in the latter part of the season. In modern agricultural monocultures, the floral resources are instead typically present for shorter periods and are not evenly distributed over the season as before. It has been suggested that reproductive output in bumblebees is particularly dependent on resource variation in the latter part of the season (Rundlöf *et al.*, 2014). In contrast, early resource peaks strongly affect the abundance of workers but not reproductive output (Westphal *et al.*, 2009). Furthermore, a weak dependence of reproductive output on resource availability during the early worker-dominated part of the colony cycle may be due to a low worker efficiency at large colony sizes (Hovestadt *et al.*, 2019). Our analysis shows that competition for floral resources among colonies has a similar effect. Our model thus supports the conclusion that a late resource peak may boost populations densities (Fig. 3d), and thus also the idea of mitigating strategies such as late-season red clover plantations.

Our finding that the ESS reproduction time does not maximize the population size can be compared with analyses of other scenarios including competitive effects on ESS phenological traits. For example, Kokko (1999) showed that prior-residence advantages in obtaining territories could cause selection of early arrival to breeding grounds in migratory birds, even though this implies arrival before the date which minimizes the survival costs. Similarly, in birds with winter flocks, reproducing ahead of the seasonal resource peak may be selected for if early hatching implies higher ranking in dominance hierarchies (Johansson *et al.*, 2013). These results imply that advancing seasons under global warming may lead to increasing population sizes via competitive release. Our study extends these previous results by suggesting a mechanism which instead yields a competitive advantage to phenologies that are later than the population maximizing strategy, and which implies that advanced seasonal resource peaks may lead to decreased population sizes in the short term.

Conclusion

We investigated the reproductive phenology of an annual social insect by including the following three model components in an optimal control model: (a) resource competition, (b) between-year population dynamics, and (c) frequency-dependent selection. The model was inspired by the life history of bumblebees, but the results should at least qualitatively be applicable to other annual organisms as well (e.g. annual plants). Three different strategies were compared: (1) the strategy predicted by the classic optimal control model of Macievicz and Oster (M&O) without resource competition and ecological feedback; (2) the Pop Max strategy maximizing population size, ignoring frequency dependence; and (3) the evolutionarily stable strategy (ESS) with all three model components. A general result is that the ESS is an intermediate strategy between the Pop Max and the M&O optimum (Fig. 3). To predict the response of a changing climate on the reproduction time (i.e. the switch from worker production to queen production), we studied the effects of changing the resource abundance, mortality rate, season length, and the resource and mortality peak times. All changes had a clear impact on phenology, except shifts in the mortality peak time. In all but one case, when the resource peak time was shifted, the three strategies did not respond in the same direction, highlighting the importance of considering the right measure for fitness. Future theoretical studies on the adaptation of pollinator phenology may consider: (1) stochastic variations of the environment, (2) co-evolution of competitive communities and the importance of mismatch, and (3) compound effects of changes in multiple environmental variables, including resource gaps and mortality peaks. We have nonetheless taken a few steps towards a better understanding of the evolution of reproductive phenology and the related ecological consequences of changes in climate and land use.

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REFERENCES

Becher, M.A., Twiston-Davies, G., Penny, T.D., Goulson, D., Rotheray, E.L. and Osborne, J.L. 2018. *Bumble*-BEEHAVE: a systems model for exploring multifactorial causes of bumblebee decline at individual, colony, population and community level. *J. Appl. Ecol.*, **55**: 2790–2801.

Beekman, M., Lingeman, R., Kleijne, F.M. and Sabelis, M.W. 1998. Optimal timing of the production of sexuals in bumblebee colonies. *Entomol. Exp. Appl.*, **88**: 147–154.

Bommarco, R., Lundin, O., Smith, H.G. and Rundlöf, M. 2011. Drastic historic shifts in bumble-bee community composition in Sweden. *Proc. R. Soc. Lond. B: Biol. Sci.*, **279**: 309–315.

Bryden, J., Gill, R.J., Mitton, R.A., Raine, N.E. and Jansen, V.A. 2013. Chronic sublethal stress causes bee colony failure. *Ecol. Lett.*, **16**: 1463–1469.

Burkle, L.A., Marlin, J.C. and Knight, T.M. 2013. Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, **340**: 1611–1615.

Cohen, D. 1971. Maximizing final yield when growth is limited by time or by limiting resources. *J. Theor. Biol.*, **33**: 299–307.

Cueva del Castillo, R., Sanabria-Urbán, S. and Serrano-Meneses, M.A. 2015. Trade-offs in the evolution of bumblebee colony and body size: a comparative analysis. *Ecol. Evol.*, **5**: 3914–3926.

Duchateau, M.J. and Velthuis, H.H.W. 1988. Development and reproductive strategies in *Bombus terrestris* colonies. *Behaviour*, **107**: 186–207.

Fitzpatrick, Ú., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V. *et al.* 2007. Rarity and decline in bumblebees: a test of causes and correlates in the Irish fauna. *Biol. Conserv.*, **136**: 185–194.

Forrest, J. and Miller-Rushing, A.J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **365**: 3101–3112.

Galpern, P., Johnson, S.A., Retzlaff, J.L., Chang, D. and Swann, J. 2017. Reduced abundance and earlier collection of bumblebee workers under intensive cultivation of a mass-flowering prairie crop. *Ecol. Evol.*, **7**: 2414–2422.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.*, **34**: 1–26.

Goulson, D. and Sparrow, K. 2009. Evidence for competition between honeybees and bumblebees: effects on bumblebee worker size. *J. Insect Conserv.*, **13**: 177–181.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L. and Totland, Ø. 2009. How does climate warming affect plant–pollinator interactions? *Ecol. Lett.*, **12**: 184–195.

Heinrich, B. 1976. Resource partitioning among some eusocial insects: bumblebees. *Ecology*, **57**: 874–889.

Herbertsson, L., Lindström, S.A.M., Rundlöf, M., Bommarco, R. and Smith, H.G. 2016. Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic Appl. Ecol.*, **17**: 609–616.

Holzschuh, A., Dainese, M., González-Varo, J.P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M. *et al.* 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.*, **19**: 1228–1236.

Hovestadt, T., Mitesser O., Poethke, A. and Holzshuch, A. 2019. Explaining the variability in the response of annual eusocial insects to mass-flowering crops. *J. Anim. Ecol.*, **88**: 178–188.

Johansson, J., Bolmgren, K. and Jonzén, N. 2013. Climate change and the optimal flowering time of annual plants in seasonal environments. *Global Change Biol.*, **19**: 197–207.

King, D. and Roughgarden, J. 1982. Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theor. Popul. Biol.*, **22**: 1–16.

Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.*, **68**: 940–950.

Lindh, M., Johansson, J., Bolmgren, K., Lundström, N.L., Brännström, Å. and Jonzén, N. 2016. Constrained growth flips the direction of optimal phenological responses among annual plants. *New Phytol.*, **209**: 1591–1599.

Macevicz, S. and Oster, G. 1976. Modeling social insect populations II: Optimal reproductive strategies in annual eusocial insect colonies. *Behav. Ecol. Sociobiol.*, **1**: 265–282.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aaasa, A., Ahas, R. *et al.* 2006. European phenological response to climate change matches the warming pattern. *Global Change Biol.*, **12**: 1969–1976.

Metz, J.A.J., Mylius, S.D. and Diekmann, O. 2008. When does evolution optimize? *Evol. Ecol. Res.*, **10**: 629–654.

Mitesser, O., Weissel, N., Strohm, E. and Poethke, H.J. 2007. Adaptive dynamic resource allocation in annual eusocial insects: environmental variation will not necessarily promote graded control. *BMC Ecol.*, **7**: 1–13.

Müller, C.B. and Schmid-Hempel, P. 1992. Variation in life-history pattern in relation to worker mortality in the bumblebee *Bombus lucorum. Funct. Ecol.*, **6**: 48–56.

Oster, G. 1976. Modeling social insect populations. I. Ergonomics of foraging and population growth in bumblebees. *Am. Nat.*, **110**: 215–245.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**: 37–42.

Poitrineau, K., Mitesser, O. and Poethke, H.J. 2009. Workers, sexuals, or both? Optimal allocation of resources to reproduction and growth in annual insect colonies. *Insectes Sociaux*, **56**: 119–129.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W.E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.*, **25**: 345–353.

Pyke, G.H., Inouye, D.W. and Thomson, J.D. 2011. Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects. *Ecol. Entomol.*, **36**: 511–521.

Ramula, S., Johansson, J., Lindén, A. and Jonzén, N. 2015. Linking phenological shifts to demographic change. *Climate Res.*, **63**: 135–144.

Rundölf, M., Persson, A.S., Smith, H.G. and Bommarco, R. 2014. Late-season mass-flowering red clover increases bumblebee queen and male densities. *Biol. Conserv.*, **172**: 138–145.

Schellhorn, N.A., Gagic, V. and Bommarco, R. 2015. Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol. Evol.*, **30**: 524–530.

Visser, M.E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. Lond. B: Biol. Sci.*, **272**: 2561–2569.

Visser, M.E., te Marvelde, L. and Lof, M.E. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *J. Ornithol.*, **153** (suppl.): S75–S84.

Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *J. Appl. Ecol.*, **46**: 187–193.

Williams, P.H. and Osborne, J.L. 2009. Bumblebee vulnerability and conservation worldwide. *Apidologie*, **40**: 367–387.